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LOCOMOTION IN THE PRIMITIVE PULMONATE SNAIL *MELAMPUS BIDENTATUS*: FOOT STRUCTURE AND FUNCTION

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Most land pulmonates crawl by means of muscular waves that travel along the foot from posterior to anterior. These waves, classified as direct waves by Vlés (1907), have been analyzed by Jones (1973) for the land slug *Agriolimax*. A great variety of wave types has been described for prosobranch gastropods; the most primitive type is thought to be the retrograde type, in which the waves travel in a direction opposite to the gastropod's progress (Miller, 1974; Trueman, 1975). Jones and Trueman (1970) have analyzed the mechanism of retrograde waves in the limpet *Patella* and have reviewed gastropod locomotory waves (Jones, 1975; Trueman, 1975).

The purpose of the work reported here has been to analyze the unusual locomotion of the snail *Melampus bidentatus*. This basommatophoran snail is a member of one of the most primitive families of pulmonates, the Ellobiidae. Information on its mode of locomotion may cast light on the origin of the locomotory behavior exhibited by the more advanced land pulmonates.

Although Morton (1955) indicated that land-inhabiting ellobiids, including *Melampus*, crawl in a way that others have classified as retrograde waves (Jones, 1975), my examination of events in *Melampus* locomotion has not supported that classification. Rather, *Melampus* exhibits a form of locomotion that fits neither the direct nor retrograde wave category nor any of the other locomotor categories of Miller (1974). *Melampus* locomotion consists of a repeated sequence of events, the crawl-step, in which the posterior of the foot slides along but the anterior is lifted and placed. Hydraulic forces, described by Chapman (1958; 1975) for a variety of soft-bodied animals, are an important component in the locomotion of *Melampus*. The blood is acted on by the columellar muscles as well as the intrinsic pedal musculature, and the transverse subdivision of the foot allows the posterior-to-anterior transfer of blood to be coordinated with the muscular events.

MATERIALS AND METHODS

Animal. Adult specimens of *Melampus bidentatus* Say with shell lengths of 7 to 11 mm were collected in salt marshes of Woods Hole, Massachusetts. They were maintained in large, covered fingerbowls lined with filter paper moistened with 75% sea water (Instant Ocean) and provided with napa (Chinese) cabbage and crushed eggshells. A photoperiod of 8L:16D and constant temperature of 16° C suppressed reproductive activity (Apley, 1968).

Photographic Techniques. Crawling snails were filmed with a Bolex Macrozoom 160 super 8 mm camera at 18 frames per second. Side and bottom views were obtained simultaneously by the use of mirrors.

Marking the Foot. Snails were anaesthetized according to the method of Price (1977). Three or more spots of India ink were injected just beneath the surface of the sole. The animals were allowed to recover overnight in fresh 75% sea water.

Anatomy. Pedal and columellar muscles were studied in live and narcotized snails and specimens fixed in alcoholic Bouins. Serial sections of snails quick-frozen in liquid nitrogen while crawling (Jones, 1973) provided information on the muscle contraction patterns during locomotion. The 10 μm sections were stained with Mallory's triple stain (Pantin, 1948).

Force Recordings. Snails were allowed to crawl over a plexiglass platform having a 2-mm gap into which a 1-mm bar was inserted. The bar was attached to a force transducer (Statham Micro-Scale Accessory Model UL5) connected to an amplifier (Gilson IC-MP module). The resulting forces were recorded on a chart recorder (Gilson ICT-SH). The transducer was connected so as to measure either upward and downward forces or backward and forward forces as the snail's foot passed across it. The translucent platform on which the snail crawled was positioned just above the writing surface of the recorder so that the crawling snail was filmed with the chart recorder's activity in the background. The absolute magnitude of the forces was not relevant to this analysis.

RESULTS

Stages in the crawl-step

As illustrated in Figure 1, the foot of *Melampus bidentatus* is divided anatomically into an anterior region (the propodium) and a posterior region (the metapodium) by a permanent transverse groove. The mouth region surrounded by the oral veil or lappets forms an important part of the locomotory surface.

In *Melampus* locomotion a single series of muscular events propagates along the foot at one time. I have called this mode of locomotion a crawl-step because the anterior part of the foot is lifted free of the substratum. Characteristic postures assumed by the foot during the crawl-step have been identified in frame-by-frame analysis of motion picture films of crawling snails. Postures identified with three easily recognized stages of the crawl-step are shown in Figure 1. Each stage is characterized by the following events:

Stage I. Metapodial shortening/propodial extension. The posterior third of the metapodium shortens as a single movement and the propodium simultaneously extends to its longest dimension. The head and oral veil are lifted off the substratum.

Stage II. Metapodial extension. A series of local muscular contractions within the metapodium produce one or more waves that ripple forward along the sides of the metapodium from the medial region of the metapodium toward the transverse groove. The region of the metapodium ahead of the elevations bulges outward and when the bulge reaches the transverse groove the posterior edge of the propodium is displaced upward and forward by the expanded metapodium. Mean-

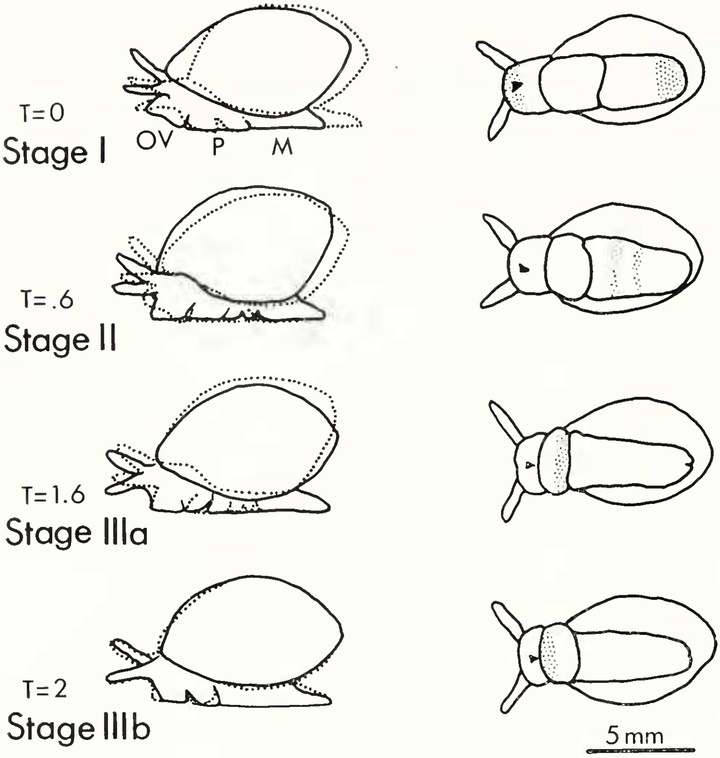

FIGURE 1. The crawl-step of *Melampus bidentatus.* Side and bottom views traced from motion picture frames for Stage I: metapodial shortening/propodial extension, Stage II: metapodial extension, and Stage III: propodial elevation, posterior (a) and then anterior (b) phase. Cumulative elapsed time in seconds is given to the left. Dotted lines (side views) give the snail's posture at onset of the movement characteristic of each stage and the unbroken lines represent the posture upon completion of the movement. Stippled regions (bottom view) indicate portions that were lifted during each stage. Subdivisions of the locomotory surface are labeled in the bottom view of Stage I: OV, oral veil-mouth region; P, propodium of the foot; M, metapodium of the foot.

while the posterior region of the metapodium narrows and flattens dorsoventrally and the shell tilts forward as the oral veil is lowered to the substratum.

Stage III. Propodial elevation. The posterior region of the propodium is elevated first (IIIa, Fig. 1) and then the anterior region is elevated (IIIb, Fig. 1). The oral veil–mouth region forms an area of contact with the substratum throughout this stage. The shell tilts backwards.

In the motion picture from which the tracings shown in Figure 1 were made, the snail progressed 2.2 mm in 2.3 sec. Snails with shell lengths of 10 to 11 mm typically crawled 2 to 4 mm/step at a rate of 10 to 20 steps/min at 20° C.

Foot morphology

Figure 2 shows the relationship of the columellar muscles to the foot. In *Melampus* the columella itself is largely resorbed during development, leaving

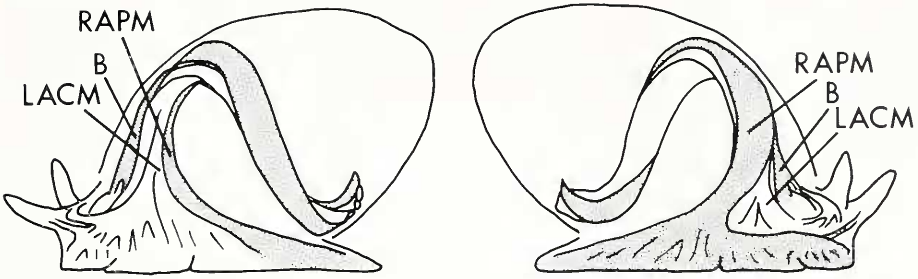

FIGURE 2. Relationship between columellar muscles and the foot in *Melampus*. A, view of animal's left side; B, right side. Left anterior cephalic muscle (LACM) is unshaded, the right anterior and right and left posterior muscle (RAPM) stippled, and buccal muscle (B) crosshatched.

the columellar muscles attached to the inner wall of the shell (Morton, 1955). The muscles follow the inner surface of the shell within the body whorl in approximately a 360° turn from origin to insertion in the extended foot. In addition to the buccal retractor muscle, two major subdivisions of the columellar muscle are apparent in *Melampus*. The left anterior and cephalic muscle (LACM, Fig. 2) originates in several adjacent bundles and further subdivides into muscle bands that insert around the head, into the left tentacle and oral veil, the left side of the propodium and approximately the anterior third of the left side of the metapodium. The right anterior and right and left posterior muscle (RAPM, Fig. 2) has a single origin on the shell and divides into muscle bands that insert on the right tentacle, the right oral veil, the right propodium, the anterior portion of the metapodium and bilaterally in the posterior region of the metapodium. Thus the muscles enter the foot in a quite asymmetrical pattern with those muscles on the left side that support the shell being the more massive. The columellar muscle system of *Melampus* probably includes both the longitudinal and columellar muscle groups described for *Lymnaea* by Plesch, Janse and Boer (1975).

In serial sections of snails quick-frozen in the act of crawling, there is no evidence that intrinsic bands of muscle fibers form discrete layers above the sole of the foot. Rather, the fibers that could be traced appear to be derived from columellar muscles. This is apparent in the parasagittal section which cuts through the left anterior and cephalic columellar muscle (Fig. 3C). The muscle fibers form a meshwork enclosing small, spherical blood spaces, shown in a region of the metapodium (Fig. 3E). These are similar to those in the foot of the limpet, *Patella* (Jones and Trueman, 1970). These small spaces are contrasted with the large blood sinuses that are present in the anterior region of the foot (Fig. 3A, D).

When sections of snails frozen in different stages of the step cycle are compared, one of the most obvious differences is in the orientation of the transverse groove. In Stage I, the metapodial shortening/propodial extension results in a propodium that is long and a transverse groove that is shallow and anteriorly-slanting (Fig. 3A). In Stage IIIa elevation of the transverse goove and posterior region of the propodium pulls the groove into a deep backward-slanting indentation (Fig. 3C). As the propodial elevation moves into the anterior propodium (Stage

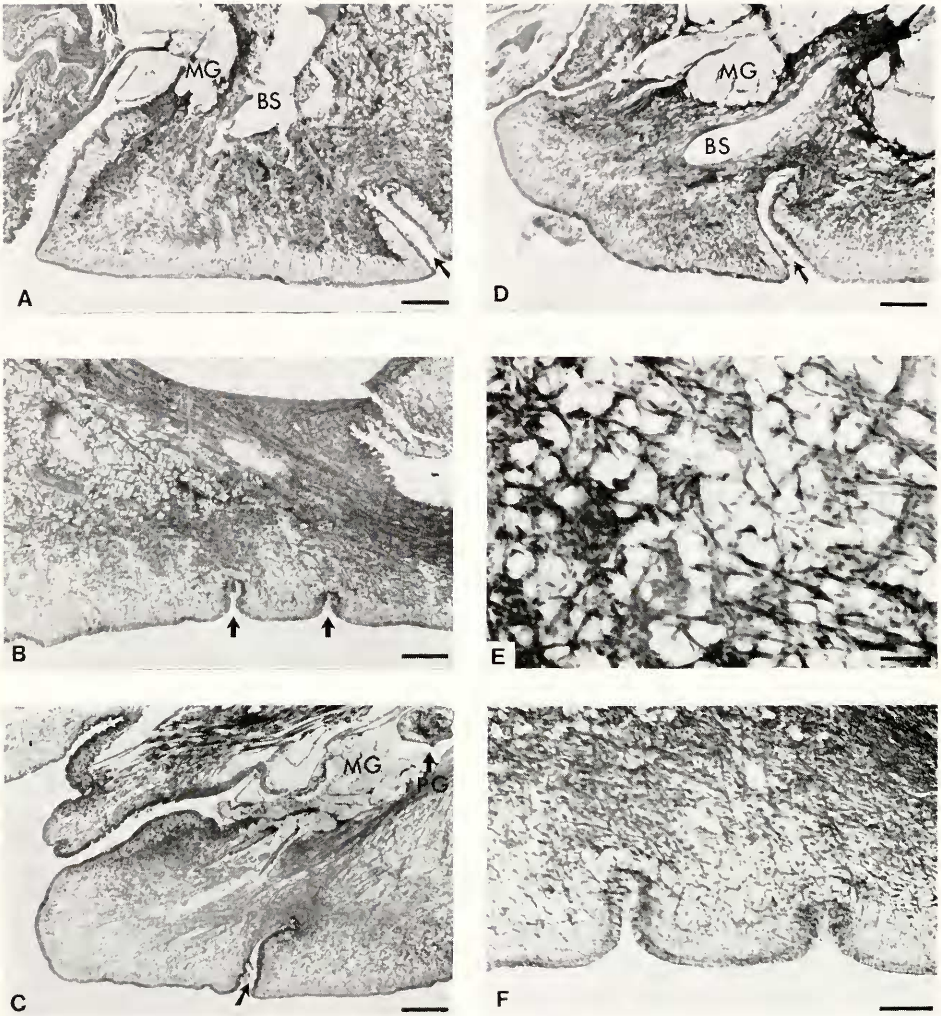

FIGURE 3. Sections prepared from specimens frozen in liquid nitrogen while crawling. In each case, anterior is to the left. A. Stage I posture, mid-sagittal section showing propodial region of foot and tranverse groove (arrow). Scale bar 250 μ. B. Stage II posture, mid-sagittal section showing metapodial region with two metapodial waves (arrows). Scale bar 250 μ. C. Stage IIIa posture, left para-sagittal section through left anterior and cephalic muscle bands in the propodial region of the foot. Arrow indicates transverse groove. Scale bar 250 μ. D. Stage IIIb posture, mid-sagittal section showing propodial region of the foot and transverse groove (arrow). Scale bar 250 μ. E. Detail of metapodial tissue showing small blood spaces. Scale bar 25 μ. F. Detail of muscle contraction pattern in the metapodial waves in Figure 3B. Scale bar 75 μ. Abbreviations used: BS, large blood sinus; MG, suprapedal mucus gland; PG, pedal ganglion.

IIIb) the transverse groove region is relaxed and assumes a condition intermediate between that of Stage IIIa and Stage I (Fig. 3D).

Metapodial contractile waves are shown in Figure 3B and the muscle pattern contributing to them is apparent at higher magnification in Figure 3F. The sole of the foot is lifted straight up rather than pulled in a slanting angle forward. It appears that the elevations are caused by a local tightening of the mesh-work of fibers within the foot. Anterior to the elevations, the blood spaces are larger than in the contracted regions behind the waves. A consequence of anterior movement of such a pattern of waves would be the forward displacement of blood.

Marked-foot experiments

In this and the following sections an attempt was made to characterize more precisely the sequence of events and the forces underlying forward progression during the crawl-step. The aim of marked-foot experiments was to analyze temporally the changes in the relative size of the propodium and metapodium and the movement of points within those regions. This was achieved by filming the foot of snails that had spots of ink injected into the sole. In every fourth frame of the film the position of the ink spots was determined, relative to a fixed point behind the snail's foot. Sample data from five crawl-steps are illustrated in Figure 4. The beginning and end of one crawl-step is included between the vertical dashed lines.

The following features are apparent from such an analysis: First, shortening of the posterior metapodium, measured as advancement of the end of the foot, is mirrored in time and magnitude by advancement of the anterior edge of the propodium. Thus during posterior shortening the length of the snail's foot does not change. The remaining events in the crawl-step are all forward shifts of intermediate points along the foot, relative to the fixed posterior and anterior

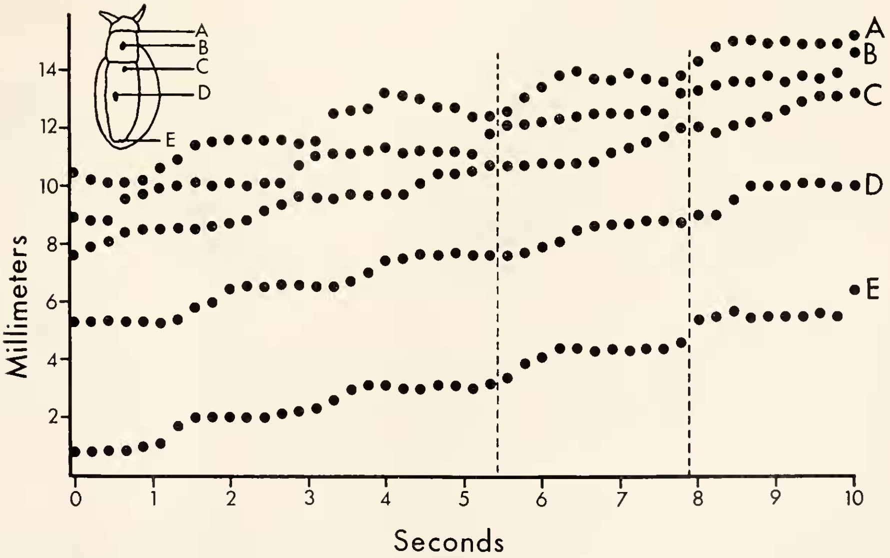

FIGURE 4. Progress of the anterior (A) and posterior (E) edges of the foot and three spots of injected ink (B-D) was charted for every fourth frame of an 18 frames/sec motion picture film. The events of one complete crawl step occur between the vertical dashed lines.

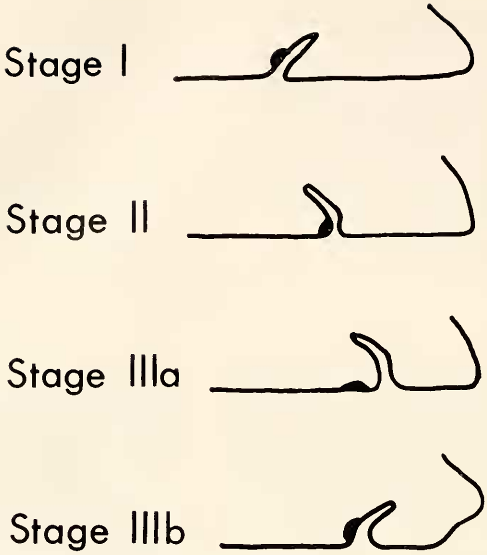

FIGURE 5. Diagrammatic illustration of the relationship of an ink spot to the transverse groove. Motion picture films indicated that during locomotion the spot of ink disappeared within the transverse groove from Stage IIIb through Stage I and was visible during Stages II and IIIa.

edges of the foot. These forward shifts proceed from posterior to anterior: the metapodial waves carry point D and then point C forward. Finally, point B moves forward as the anterior propodium is lifted off the substratum.

Films of a snail with a differently placed ink spot shed light on events occurring in the region of the transverse groove during locomotion. The ink spot was in the anterior metapodium almost within the transverse groove. During locomotion, the spot appeared and disappeared with each crawl-step. The position of the spot during the crawl-step is illustrated diagrammatically in Figure 5. It became visible during metapodial extension in Stage II and was eclipsed by expansion of the posterior propodium as the anterior propodium was elevated (Stage IIIb). Both this and the histological evidence indicate that although the transverse groove is a constant feature of the foot, a greater or lesser region of the pedal sole anterior or posterior to this region can be drawn up into the groove. Both changes in blood volume in the propodium and metapodium adjacent to the groove, and contraction of columellar muscles which insert close to the groove, alter its configuration.

Upward and downward forces

Direct observations and motion picture films indicate that portions of the *Melampus* foot are elevated during locomotion. Forward sliding movements along the mucus-covered substratum might also be expected to exhibit an upward component. Transducer recordings of upward and downward forces were obtained to determine which portions of the sole are experiencing upward or downward (weight-bearing) forces during each stage in the crawl-step cycle.

The forces exerted during locomotion were measured as snails crawled across a moveable bar positioned in a slit in a plexiglass platform. Five to six step cycles were required for snails to crawl across the bar and therefore at each successive step the transducer measured forces from a more posterior region of the foot. The pattern of upward and downward deflections recorded in this manner was fairly constant from crossing to crossing and animal to animal. Figure 6A is typical of the recordings that were produced. These data were interpreted as described in the methods. Postures characteristic of Stages I–III for each step were identified with particular points on the force recording as illustrated in Figure 6A.

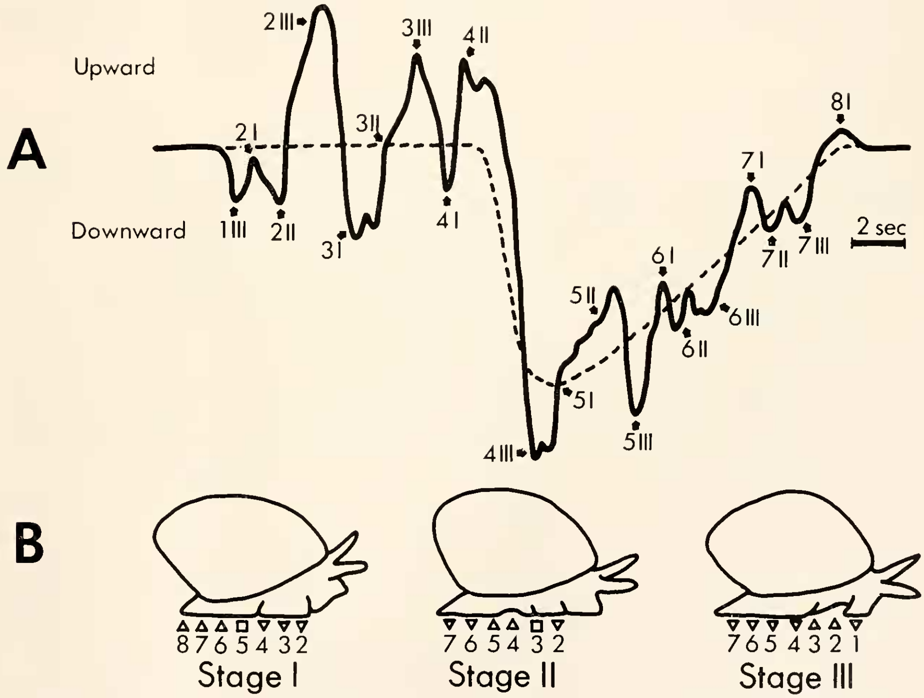

FIGURE 6. A is the force transducer recording of upward and downward forces exerted on a bar as a snail crawled across it. A portion of the snail's foot was in contact with the bar for six complete steps and the end and beginning of two other steps, for a total of 24 sec. Each point at which the simultaneously-recorded motion picture film indicated that the snail assumed one of the postures characteristic of Stage I, II or III of the crawl step cycle was marked on the transducer recording. The dotted line represents a baseline adjustment that was inserted to compensate for the overwhelming effect of passage of the shell mass onto the bar. In B the information obtained from the force recording is represented as a pattern of upward and downward-pointing triangles showing the distribution of vertical forces exerted by the foot on the substratum at Stages I, II and III of the step cycle. Regions exerting no vertical force are indicated by squares. The position of the triangles or squares under the foot marks the position of the recording bar each time the posture characteristics of a particular stage was assumed.

Note that in the force recording in Figure 6A there is a dramatic downward registration following stage II of the fourth step. At that time the shell weight shifts forward onto the bar. From then until the foot is pulled off the bar, all the upward deflections fail to rise above the original baseline. The dotted line in Figure 6A was inserted as a relative baseline in an attempt to correct for the overwhelming effect of shell weight on the force recordings. Using that correction, the results of these experiments were summarized in Figure 6B. The following conclusions can be drawn: In metapodial shortening/propodial extension the propodium is weight-bearing while the posterior region of the metapodium exerts an upward force on the substratum. In metapodial lengthening the anterior region of the propodium and the posterior region of the metapodium are weight-bearing while the waves moving forward in the anterior region of the metapodium exert an upward force. In propodial elevation the oral veil and the entire metapodium are weight-bearing during elevation of the posterior and anterior propodium.

Forward and backward forces

Lissmann (1946) defined the sliding progression of a snail's foot along a substratum as being the product of forces acting parallel to the ground, including internal and external forces acting to change the shape of the snail's body and the reactions from the ground. The concept of the internal forces has been advanced and direct measurements of fluid pressure made for a variety of animals since that time (see Chapman, 1975). The reactions of the ground to the passage of the snail's foot were measured in this study to indicate what was happening along the length of the foot at each stage in the crawl-step cycle. Lissmann's (1946) reactions from the ground were defined as the static reaction, which is the force exerted on the substratum in a backward direction by stationary areas while other regions of the foot are advanced, and sliding friction, which is the forward force that moving portions of the foot exert. These backward and forward forces were recorded and interpreted in a manner similar to that described for upward and downward forces, but with the transducer measuring forces in the horizontal plane.

In general the sole of the foot did not noticeably protrude into the space in the plexiglass slit adjacent to the recording bar, but rather moved smoothly onto the bar. There were two notable exceptions to this generalization: if the spacing of the animal's approach to the bar was such that anterior metapodial advancement or propodial advancement began at the edge of the slit, then the foot region bulged downward into the gap and thereby displaced the bar forward by pushing it from behind. A sample recording of the forward and backward forces is shown in Figure 7A. The labels on the recording show the points at which the snail's posture matched the characteristic postures for stages I, II, and III in each of the six crawl steps. The distribution of forces beneath the foot at each stage is illustrated in Figure 7B. During metapodial shortening/propodial extension, the posterior metapodium and the anterior propodium register forward sliding friction while the anterior metapodium and posterior propodium show the static reaction. In metapodial extension the entire metapodium registers a forward force and the propodium registers a backward force. In propodial elevation the propodium is the only region showing forward sliding friction.

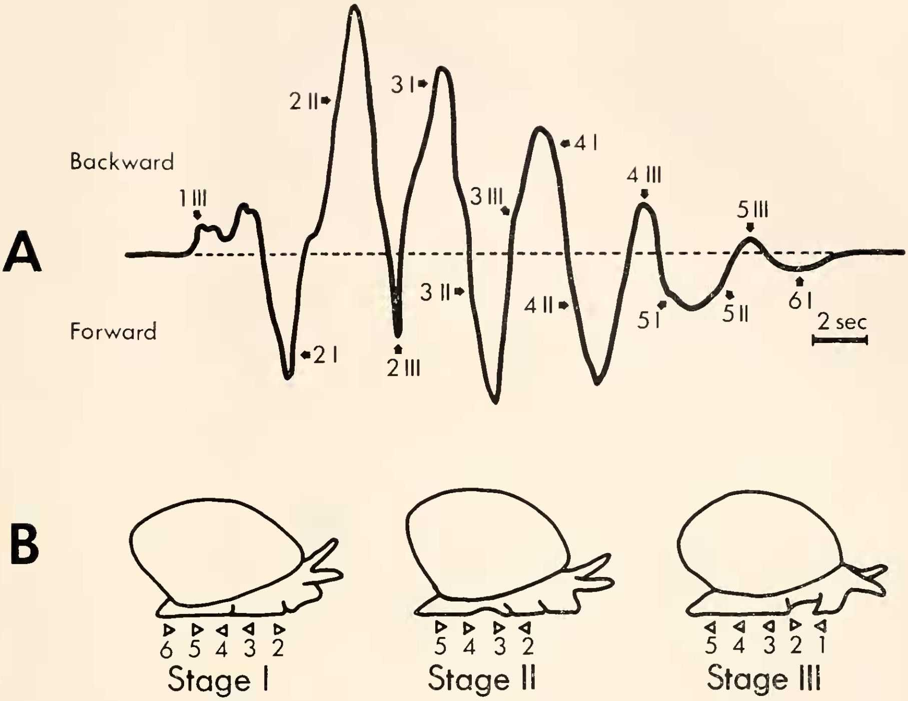

FIGURE 7. A is the force transducer recording of forward and backward forces exerted by a snail's foot as it crawled across a bar. The snail required four complete crawl-step cycles and portions of two other cycles to complete the crossing. Information was obtained in a manner similar to that described for Figure 6. B is the pattern of forward and backward forces exerted by the foot on the substratum in Stages I, II and III of the crawl-step.

DISCUSSION

The crawl-step of *Melampus* is a complex sequence of events compared with the direct pedal waves of most land pulmonates. Figure 8 gives a model for *Melampus* locomotion that was constructed from the histology, cinematography and force transducer recordings presented in the results.

According to this model the Stage I metapodial shortening/propodial extension result from a single muscular event: contraction of columellar muscles in the posterior half of the metapodium. This action not only draws the end of the foot upward and forward, as indicated by the transducer recordings, but it causes some blood to leave the posterior region of the foot. This blood could flow across the low transverse groove into the propodium and into the anterior region of the body. The pattern of forces recorded from the foot at this stage indicates that the weight is primarily borne by the posterior propodium and that it and the anterior metapodium experience a backward drag (the static reaction). The combination of downward and forward forces recorded from the anterior propodium are what would be expected in a region experiencing invasion of blood from the posterior. The observation that the propodium bulged downward into the crack

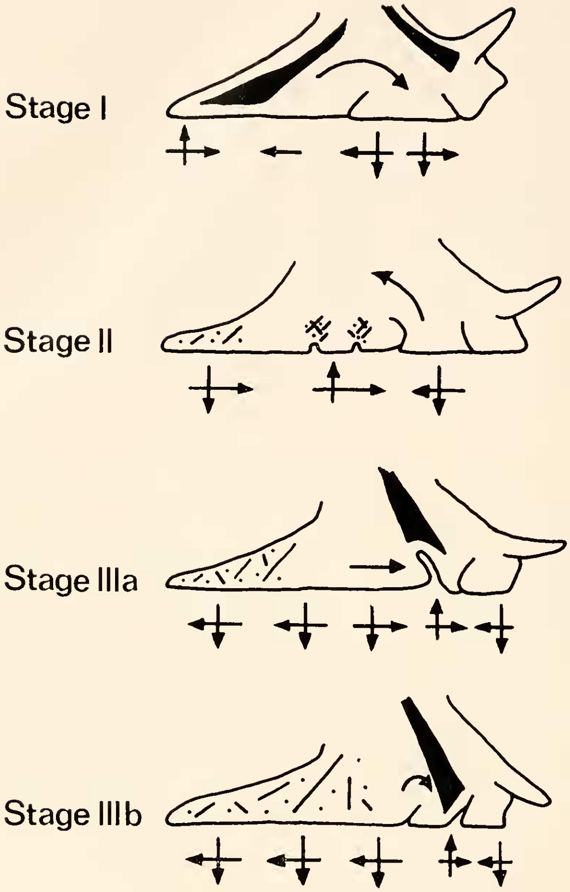

FIGURE 8. Model of mechanical events producing locomotion in *Melampus*. Arrows below the foot show forces exerted on the substratum; arrows within the body show fluid dynamics; dark regions in the body indicate muscle contraction patterns. See text for discussion.

adjacent to the recording bar indicates that relaxed tonus in the propodium may contribute to the hydraulic expansion.

In Stage II, metapodial extension is produced by low-amplitude waves travelling from the middle toward the anterior metapodium. Their action is depicted as squeezing blood forward within the ventral portion of the foot until it accumulates behind the transverse groove. The resulting change in orientation of the groove causes blood in the posterior propodium to move up into the large blood sinuses in the dorsal propodium and anterior metapodium. The snail's weight rests on the anterior propodium and the posterior metapodium while the middle of the foot shifts forward. The observed narrowing of the metapodium that begins in this stage and continues through Stage III probably exerts a tonic force on the blood and favors forward movement of the foot. This tonic force may be produced by body wall musculature rather than by pedal muscle fibers derived from the columellar muscles.

In Stage III, propodial elevation results from contraction of columellar muscle bands, chiefly those of the left anterior and cephalic columellar muscle. The transverse groove region is elevated in Stage IIIa. This allows the anterior edge of the metapodium to expand into the space formerly occupied by the posterior propodium. Again, the combination of downward and forward forces indicates that metapodial extension results from an hydraulic event. By Stage IIIb the more anterior region of the propodium is elevated by columellar muscles and the posterior region returns to the substratum in advance of its former position. This forward displacement is due, at least in part, to the extension of the metapodium in Stage IIIa. Throughout Stage III the oral veil and the posterior metapodium are static, weight-bearing regions that support the forward progression of the anterior region of the foot.

The hydraulic expansion of the anterior region of the foot of *Melampus* is similar to hydraulic events described for burrowing in the naticid snail *Polinices josephinus* (Trueman, 1968). The work of Schiemenz (1884) and, more recently, Russell-Hunter and Russell-Hunter (1968) and Russell-Hunter and Apley (1968) revealed that in naticids water is taken up into special channels to aid in the expansion of the foot. Both the burrowing *Polinices* and the crawling *Melampus* advance in a similar stepwise fashion.

The deeply cleft transverse groove and elevation of the propodium in a stepping locomotion are features that have arisen independently in several lines of Ellobiidae that are adapted to a hard substratum (Morton, 1955). Morton (1955) suggests that it may be especially adaptive in progression over broken or irregular surfaces. The model presented above indicates that the transverse groove has a valve-like function, rendering the metapodium relatively independent of the propodium during metapodial extension. This enhanced control over hydraulic events may have been important in the transition from the marine habitat to land in the Ellobiidae.

Morton (1955) describes the locomotion of ellobiids with a divided foot as ". . . fixing down the anterior third of the foot well in advance of the animal and drawing the remainder forwards upon it" (p. 151). This brief description neglects the hydraulic expansion of the propodium and thereby exaggerates the superficial similarity between *Melampus* locomotion and the "loping" locomotion of another primitive pulmonate, *Otina otis*. According to Vlés' (1913) account of *Otina* locomotion, the transversely subdivided foot is used in a stepping fashion in which the anterior is lifted and placed forward, rendering the foot long, and then the posterior is pulled forward, rendering the foot short. The hydraulic component that is responsible for maintaining the *Melampus* foot at a relatively constant length is apparently absent in *Otina* locomotion. Furthermore, no matter in what order the events of *Melampus* locomotion are considered, the contraction pattern within the propodium clearly passes from posterior to anterior and therefore the crawl-step locomotion exhibited by this snail cannot be considered a retrograde wave. Thus the locomotion of *Melampus* cannot be cited to support the supposition that the retrograde wave locomotion seen in stylommatophoran gastropods during escape behavior is a primitive type of locomotor behavior within the pulmonates.

The only feature of *Melampus* locomotion that is similar to the locomotion of higher land snails and slugs is the anteriorly-travelling ripple that produces metapodial lengthening. This wave of contraction is apparently produced by intrinsic pedal musculature and, although the *Melampus* foot appears to lack the specialized musculature that produces the waves in *Agriolimax* (Jones 1973), observation of the side view clearly shows that the elevated region of the wave is compressed and its forward movement forces a bolus of fluid forward. The fact that these metapodial waves do not originate at the end of the foot is very significant in an attempt to relate them to the direct waves of stylommatophorans. This is the case because, as Jones (1975) has pointed out, the multiple direct wave pattern of higher pulmonates could not be derived by adding waves to the single direct wave type of locomotion such as that exhibited by *Onchidella,* in which the wave begins by shortening of the posterior region of the foot (Vlés, 1907). Such an action renders the foot shorter during locomotion than when it is at rest and the propagation of many waves at the posterior of the foot before the first wave passes off the anterior would cause the foot to become prohibitively short. The wave pattern in higher pulmonates, in contrast, is initiated at the onset of locomotion at a site near the anterior part of the foot, where constriction of the elevated region results in a compensatory stretching of a more posterior part of the foot and the foot length remains constant (Lissmann, 1945; Jones, 1975). Thus the metapodial waves of *Melampus* could represent the survival of the motor pattern that gave rise to multiple direct wave locomotion in stylommatophorans. Morton's (1955) description of locomotion in ellobiids that lack a transverse groove suggests that this wave pattern may be more pronounced in less specialized members of the family.

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SUMMARY

The foot of *Melampus* is subdivided into an anterior propodium and a posterior metapodium by a permanent transverse groove. Locomotion in *Melampus* consists of repetition of a cycle of events that pass from posterior to anterior; this cycle has been named a crawl-step Three stages in the crawl-step have been identified: Metapodial shortening is produced by the action of columellar muscles and this action forces blood anteriorly to extend the propodium. Metapodial lengthening is produced by muscle action within the metapodium and extends the metapodial region forward at the expense of the propodium. Propodial elevation is produced by columellar muscles and prepares the propodium to "step" forward while fluid invasion occurs in the first stage.

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